Analysis of the Frequency of *Lechriodus intergerivus* Tyler (Anura: Leptodactylidae) in Oligo-Miocene Local Faunas of Riversleigh Station, Queensland

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Lechriodus intergerivus Tyler, 1989 occurs in large numbers in Oligo-Miocene fossil deposits on Riversleigh Station, in northwestern Queensland, dominating the Riversleigh frog faunas in which it occurs. The abundance of *L. intergerivus* in the Riversleigh fossil deposits does not appear to reflect either dry condition aggregates or breeding congregations, but rather the relative abundance of this species in local frog faunas. The frequency of *L. intergerivus* in the Riversleigh sites appears to broadly correlate with the age of the sediments in which it occurs: the proportion of *L. intergerivus* is higher in Riversleigh's early to middle Miocene sites (up to 80.8% of frogs) than in middle to early late Miocene deposits (as low as 35.5%). Changes in forest habitat in the Riversleigh area during the Miocene may have contributed to the observed decline in numbers of *L. intergerivus*.

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INTRODUCTION

Lechriodus intergerivus Tyler (1989) was described from 190 ilia recovered from fossil-rich Oligo-Miocene freshwater limestone deposits on Riversleigh Station in northwestern Queensland. It represents the second Tertiary leptodactylid (myobatrachid) reported from Australia. At the time of the preparation of the description 397 frog ilia had been recovered from the Riversleigh deposits, of which 50% represented *L. intergerivus*.

Subsequent preparation of more of the Riversleigh Oligo-Miocene limestone in the School of Biological Science at the University of New South Wales has produced many more frog specimens that confirm this observation. The total number of ilia recovered has doubled to 777, of which 420 are *L. intergerivus*, (54% of the total).

Given that there are at least 15 frog species in the Riversleigh Oligo-Miocene faunas (Tyler, unpubl.), a variety of reasons could be postulated to explain the prevalence of this species in the Riversleigh fossil record. Here we document the incidence across the ten sites where we consider sample sizes to be adequate, and explore the palaeoenvironmental implications of the observations.

INCIDENCE

In a sequence of fossil deposits on Riversleigh, which spans the last 25 million years, more than 100 local faunas or fossil assemblages are now recognized (Archer *et al.*, 1989). The majority of these local faunas are of Oligo-Miocene age, i.e. approximately 15-25 million years old. *Lechriodus intergerivus* has been recorded from 20 of Riversleigh's Oligo-Miocene local faunas. At each of ten of these sites at least 15 frog ilia have been recovered. The incidence of *L. intergerivus* at those ten is expressed in Fig. 1 as a percentage of ilia recovered from each site. The lowest incidences occur at Gag and Henk's Hollow Sites (35.5 and 35.8% respectively) and the highest at Wayne's Wok Site (80.8%).

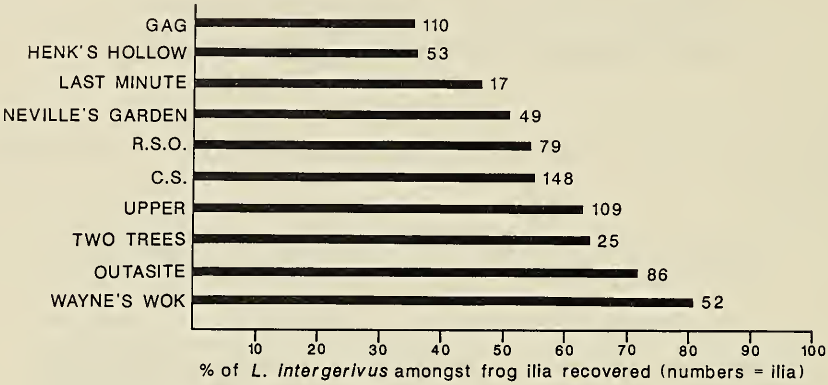

Fig. 1. Incidence of *Lechriodus intergerivus* at ten sites in the Riversleigh Oligo-Miocene faunas.

Archer *et al.* (1989) have identified three primary intervals of Oligo-Miocene deposition at Riversleigh which they define as Systems A-C, System A being late Oligocene to early Miocene in age, System B possibly early to middle Miocene and System C middle to early late Miocene in age. The frequency of *L. intergerivus* in these sites appears to broadly correlate with the age of the sediments in which it occurs. For at least Riversleigh's Systems B and C, the older the local fauna, the higher the proportion of *L. intergerivus* among its frogs. Wayne's Wok, Outasite, Upper, CS and RSO Sites occur within Riversleigh's Sytem B sediments, while Last Minute, Henk's Hollow and Gag Sites are part of the younger System C (Archer *et al.*, 1989). *Lechriodus intergerivus* has not been recorded from System A sites.

There are two notable exceptions to the observed pattern. From Two Trees Site, a System C site, a relatively high proportion of *L. intergerivus* has been recovered. From Neville's Garden Site, the proportion of *L. intergerivus* retrieved is relatively low, yet the deposit is interpreted to be among the oldest of System B sites (Archer *et al.*, 1989).

Discussion

Two particular aspects of these observations merit discussion: the overall high incidence of *L. intergerivus* in all 10 sites; and the variation in incidence between sites.

Unless *L. intergerivus* was in some way selectively favoured for fossilization by an unknown process, it would appear that its predominance at the sites is not an artefact, but a reflection of its relative abundance.

Two behavioural characteristics of frogs can lead to high densities of single species at a particular site: localized breeding congregations, and aggregations to reduce water loss during dry conditions.

Non-breeding aggregations have been documented in numerous leptodactylid and hylid species, e.g. *Limnodynastes fletcheri* (Tyler, 1976), *Taudactylus diurnus* (K. R. McDonald, pers. comm.), *Litoria caerulea* and *L. rubella* (Slevin, 1955) and *L. coplandi* (Miles, 1988).

Considering the possibility that the high numbers were the result of aggregation during dry conditions, the palaeoenvironment of the late Oligocene to middle Miocene of the Riversleigh area is interpreted by Archer *et al.* (1989) to have been lush, lowland rainforest with a partially open understory, and hence dry conditions as such are unlikely to have led to aggregations of this single species.

Within our experience, dense breeding populations in Australia are almost inevitably composed of mixed species. Nevertheless predominance of any one species could on occasions amount to perhaps one-third of the mixed population (at the lower end of the range that we report). *Litoria chloris* is an example of a species that will breed in shallow water in enormous numbers in the absence of any other species (McDonald, Seymour, Davies and Tyler, unpubl. 1976).

Extant species of *Lechriodus* are moderate sized frogs restricted to temperate and subtropical rainforests of New Guinea (three species) and northeastern New South Wales and southeastern Queensland (one species: *L. fletcheri*). Biological data on extant *Lechriodus* species are confined to details of the life history of *L. fletcheri*. Eggs are deposited in foam nests often hidden from direct light. The deposition site commonly is small bodies of water with limited food, and the tadpoles are carnivorous and often cannibalistic (Moore, 1961; Martin, 1967; Tyler unpubl.). Perhaps as a consequence of the spatial separation of the egg clumps, *L. fletcheri* does not form large breeding congregations. The likelihood of simultaneous fossilization of breeding congregations not explaining the dominance of *L. intergerivus* at Riversleigh Station, is further supported by the presence of diverse sizes in the samples, which are therefore not confined to adults, as would occur in a breeding congregation.

Considering the differences in density per site, it is possible that progressive changes in climate could account for most of the observed changes. As noted above, Archer *et al.* (1989) interpret the palaeoenvironment of the Riversleigh area during the Oligo-Miocene to have been rainforest. Subsequent and progressive drying and cooling of northern Australia during the remainder of the Tertiary and Quaternary brought dramatic changes to the area. By Pliocene-Quaternary time, Riversleigh species-level and family-level diversity had fallen. This is most evident among mammals, and appears to reflect the collapse of local rainforest communities and their replacement by open forest savannah habitats (Archer *et al.*, 1989).

Evidence from the Riversleigh faunas, and other northern Australian fossil faunas such as the Northern Territory's Bullock Creek Local Fauna and Alcoota Local Fauna (Woodburne *et al.*, 1985), suggests that these changes began as early as the middle to late Miocene, i.e. during Riversleigh's Systems B-C time.

The decline in numbers of *L. intergerivus* in Riversleigh's System C deposits may reflect a decline in moist, rainforest habitat, or at least a particular component of that habitat, resulting from broad changes in forest and animal communities occurring across northern Australia during the middle and late Miocene.

It is also apparent that the immediate depositional environment of a fossil site influences its faunal composition. At Riversleigh, many different depositional mechanisms appear to have been responsible for producing the variety of Oligo-Miocene sediments observed.

Some deposits evidently accumulated inside caves, others outside in the forest in shallow or deep water. Depositional environments at most of the sites containing *Lechriodus* are interpreted to have been broadly similar: relatively small, spring-fed, lime-rich pools occurring in rainforest-covered karst country. Upper Site is probably the best studied of this kind of Riversleigh deposit and also one of the richest. Animals recovered from 1.5 tonnes of Upper Site limestone include 64 species of mammals, as well as diverse assemblages of birds, reptiles, frogs, fish and even invertebrates (Archer *et al.*, 1989). Thirteen species of frogs have been recorded from Upper Site: six leptodactylid species (*L. intergerivus*, *Crinia* sp., two species of *Kyarranus* and two *Limnodynastes*) and eight hylid species (*Litoria* spp.) (Archer *et al.*, 1989). Conditions at such sites evidently favoured *L. intergerivus*, which at Upper Site comprises 63% of the frog fauna.

On the other hand, *L. intergerivus* is noticeably absent from a number of Oligo-Miocene deposits interpreted to have accumulated in large or deep pools. For example, this species has not yet been found at sites such as Ringtail, Bob's Boulders, Crusty Meat Pie and Quentin's Quarry, relatively well-sampled System C deposits interpreted to have been deep pools supporting large individual fish, crocodiles, turtles and sometimes platypuses. Nor has it been found in System A sites. The palaeoecological model proposed by Archer *et al.*, (1989) for System A deposits (e.g. Site D and equivalents such as Sticky Beak and White Hunter Sites) is a large, spring-fed lake, fringed by lush rainforest, that filled the central basin of the Riversleigh area. Perennial streams or periodic rushes of surface water may have fed the lake from surrounding forested terrain. Today, *L. fletcheri* chooses small bodies of water in which to deposit its eggs. That water depth might have always been an important limiting factor for *Lechriodus* is an hypothesis testable by continued study of these sites and their faunas.

For many other deposits, understanding about local conditions is still rudimentary. This is certainly true for both Neville's Garden Site and Two Trees Site. Neville's Garden appears to have provided less suitable habitat for *L. intergerivus* than other System B sites, while Two Trees Site provided far more suitable conditions than all other System C sites. Preliminary investigations of these sites and their faunas suggest that the Neville's Garden deposit accumulated in a pool just outside a cave (the depth and extent of this pool is as yet unknown), while the Two Tree deposit remains an enigma. The latter is associated with a thick bed of horizontally laminated travertine and, more curiously, it contains the potoroid marsupial *Bettongia moyesi*, the only occurrence of the genus in the Tertiary record (Flannery and Archer, 1987). Further study of these sites and their faunas will be important in identifying factors affecting Riversleigh's fossil frog communities and defining the microhabitat requirements for *L. intergerivus*.

In summary, the predominance of *L. intergerivus* in many of Riversleigh's Oligo-Miocene fossil deposits appears to reflect its relative abundance in local frog faunas, rather than breeding congregations or aggregations resulting from dry conditions. The frequency of *L. intergerivus* in the Riversleigh deposits correlates with two factors: water depth and age of deposit. Shallow (rather than deep) water environments appear to have been the preferred habitat for *Lechriodus intergerivus*. Within this habitat *L. intergerivus* is more abundant in older rather than younger Riversleigh deposits, the marked decline in the species' abundance being attributed here to changes in forest habitat in the Riversleigh area during the Miocene.

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